Control of human mandibular posture during locomotion

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Mandibular movements and masseter muscle activity were measured in humans during hopping, walking and running to determine whether reflexes contribute to the maintenance of jaw position during locomotion. In initial experiments, subjects hopped so that they landed either on their toes or on their heel. Landing on the toes provoked only small mandibular movements and no reflex responses in the masseter electromyogram (EMG). Landing on the heels with the jaw muscles relaxed caused the mandible to move vertically downwards relative to the maxilla, and evoked a brisk reflex response in the masseter at monosynaptic latency. Neither this relative movement of the mandible nor the reflex was seen when the teeth were clenched: hence the reflex is not the result of vestibular activation during head movement. The same variables were measured in a second series of experiments while subjects stood, walked and ran at various speeds and at various inclinations on a treadmill. During walking, the vertical movements of the head and therefore the mandible were slow and small, and there was no tonic masseter EMG or gait-related activity in the jaw-closing muscles. When subjects ran, the vertical head and jaw movement depended on the running speed and the inclination of the treadmill. Landing on the heels induced larger movements than landing on the toes. About 10 ms after each foot-strike, the mandible moved downwards relative to the maxilla, thereby stretching the jaw-closing muscles and activating them at segmental reflex latency. This caused the mandible to move back upwards. The strength of the reflex response was related to the speed and amplitude of the vertical jaw movement following landing. It is concluded that, during walking, the small, slow movements of the mandible relative to the maxilla are subthreshold for stretch reflexes in the jaw muscles: i.e. the mandible is supported by visco-elasticity of the soft tissues in the masticatory system. However, the brisker downward movements of the mandible after heel-landing during hopping and running evoke segmental reflex responses which contribute to the active maintenance of the posture of the mandible. This is a unique demonstration of how a stretch reflex operates to maintain posture under entirely natural conditions.

In a person who is sitting or standing still, the vertical position of the mandible remains fairly stable with respect to the maxilla: this is the so-called 'rest' position of the mandible, which is an important point of reference in dentistry and reconstructive maxillofacial surgery. Despite much debate, it is still unresolved whether the mandible is actively supported against gravity in this relatively stable vertical position by tonic contraction of the jaw-closing muscles or is passively supported by the visco-elastic properties of soft tissues (Lynn & Yemm, 1971; Møller, 1976; Michelotti *et al.* 1997; Peck *et al.* 2002). This question has not been resolved by simple observation of either surface or intramuscular electromyogram (EMG)

records in subjects even in a person sitting upright at rest. Attempts to determine whether the mandible is actively supported in this position by reflex activity (Møller, 1976; Goldberg & Derfler, 1977) have given ambiguous results because of the difficulty in detecting very low levels of activity in the jaw-closing muscles which would resist gravity when the head is upright. In a recent review, Woda *et al.* (2001) concluded that both passive visco-elastic forces (e.g. Yemm & Berry, 1969; Peck *et al.* 2002) and tonic activity in the jaw-closing muscles acting as a 'position servo' (e.g. Møller, 1976; Goldberg & Derfler, 1977) probably contribute to the support of the mandible against gravity in its rest position in stationary subjects.

However, we have found no evidence for reflex control of the mandibular rest position in subjects sitting upright (Jaberzadeh *et al.* 2003). The low-amplitude tremor that can be demonstrated in the masticatory system is not the result of reflex servo-control of jaw position, but arises from weak, alternating activation of the jaw-opening and closing muscles that is generated by an oscillator within the central nervous system. That study concluded that the jaw is supported primarily by passive forces when the head is stationary.

This raises the question of whether the mandible is supported actively during brisk vertical head movements. It has recently been shown that the vertical position of the mandible relative to the maxilla moves up and down within a small range during locomotion (Shiller *et al.* 2001; Flavel *et al.* 2003). Common experience indicates that the teeth do not come into contact with each step even during vigorous running, which suggests that there is some active (i.e. reflex) control of mandibular vertical position when the head moves up and down in locomotion.

The jaw-closing muscles are known to have sensitive short- and long-latency stretch reflexes (Poliakov & Miles, 1994); hence we hypothesized that stretch of the jaw-closing muscles during locomotion induces reflex responses in these muscles which tend to restore the mandible towards its rest position when it is displaced during head movements.

In the present study, the vertical position of the mandible was monitored at rest and during various forms of locomotion, and was correlated with the activity in its main antigravity muscle, the masseter. The kinematic data obtained during a subset of the experiments in this study are reported in detail elsewhere (Flavel *et al.* 2003).

Methods

This study was conducted with the approval of the Human Research Ethics Committee of the University of Adelaide, and conformed to the principles of the Declaration of Helsinki. The subjects were aged 18–51 years and had no relevant medical or dental history. All gave informed, written consent.

Movements of the head and the mandible were measured using a method developed in this laboratory (Flavel *et al.* 2002). Briefly, small accelerometers were glued to the upper and lower incisor teeth with glass ionomer dental cement (GC Fuji IX GP, GC Corporation, Tokyo, Japan). The outputs of these matched accelerometers were recorded separately, band-pass filtered (DC to 500 Hz), and summed electronically in a differential amplifier. The

difference between their outputs gave acceleration of the mandible relative to the head. A small Hall-effect device was also incorporated into the system to give a record of the separation between the upper and lower teeth. Mandibular velocity relative to the head was obtained by integrating the differential acceleration signal.

A separate accelerometer taped to the right ankle indicated foot-strike during locomotion.

The EMG of the right masseter muscle was recorded with surface electrodes placed along the long axis of the muscle. EMG signals were filtered (sixth-order Butterworth, bandwidth 50–500 Hz), and all signals were recorded continuously on digital tape during the various manoeuvres described below.

The latency of the monosynaptic reflex response to stretch of each subject's jaw-closing muscles was determined by tapping briskly with a tendon hammer on a finger placed on the chin. An accelerometer in the tendon hammer indicated the time of impact.

Hopping

In the initial experiments on hopping, head acceleration was measured with an accelerometer attached to tightly fitting welding goggles whose frame was moulded to the face and which was held in place by a head strap, rather than with the accelerometer mounted on an upper incisor tooth. Eight healthy male subjects hopped barefoot on one leg on a force plate. Each run consisted of 100 hops at one hop per 2 s. After every 25 hops, the subjects rested for about 2 min, then changed to hopping on the other leg to reduce fatigue. The hopping height was approximately 100 mm, and subjects held their head erect and maintained a forward gaze. In different runs, subjects deliberately landed on either the toe or the heel of one foot.

In a separate series of trials, subjects kept their teeth firmly clenched together to prevent jaw movement while they hopped a further 100 times and landed on their heels. This clench gave a masseter EMG level approximately 10% of that produced in a maximal voluntary contraction.

Locomotion

In the second series of experiments on a different group of eight male and four female subjects, the EMG and kinematic variables were recorded while subjects stood, walked and ran barefoot on a motorized treadmill (Tetley Heartmaster Mk 2, Tetley Electronics, Sydney). After some practice, each subject walked or ran forwards for 4 min while the treadmill was activated at speeds of 0.7, 1.4, 2.1

and 2.8 m s^{-1} (2.5, 5. 7.5 and 10 km h^{-1}). Subjects rested for at least 2 min between every run. The subjects ran again at the same speeds when the inclination of the treadmill was changed to a 5 deg negative slope ('downhill') and then again with it set to a 5 deg positive inclination ('uphill'). Subjects were instructed to keep their head erect and to gaze forward at a target placed at eye level at 2 m distance, and to maintain a comfortable, relaxed facial and jaw posture. They were constantly monitored and given verbal feedback to assist with this.

The data were analysed off-line with a computer-based laboratory interface (1401plus, CED Ltd, Cambridge, UK) which sampled all signals at 5 kHz. Whenever possible, the downward acceleration of the mandible relative to the maxilla was used to trigger an ensemble average of the rectified and unrectified EMG signals from the jaw-closing muscles, and the various kinematic variables during locomotion. However, in the paradigms that caused only very small mandibular movements (walking, toe-landing when hopping, and heel-landing with the teeth clenched), the averager was triggered with the foot-strike signal from the force-plate.

ANOVA was used to assess the effect of treadmill speed on the size of masseter EMG reflex responses and peak downwards displacement of the mandible following landing. Scheffe's test was used for *post hoc* comparisons, where indicated. For all comparisons, significance was reported for $P < 0.05$.

Results

The pattern of responses in all subjects during the various manoeuvres was very similar, and is therefore illustrated by records obtained from individual subjects.

Hopping

Hopping and landing on the toes of one leg was a familiar and comfortable task for all subjects. However, landing on the heels was unfamiliar, and uncomfortable because it resulted in a strong jolting of the head. The ground reaction forces and the transmission of these to the skull in the three hopping tasks are shown for a representative subject in Fig. 1. During toe-landing (left column), the footplate record showed an initial brisk deceleration upon initial toe contact, followed by a slow phase of deceleration as the impact of landing was absorbed by the muscles of the leg. Hence, much of the shock of landing was absorbed before it reached the skull. About 10 ms after the initial heel impact, the mandible also began to decelerate. This small, slow, vertical displacement did not evoke a reflex response in the masseter in any subject.

When the same subject landed heel-first (Fig. 1, middle column), the deceleration measured at the footplate was about 10 times greater than in toe-landing. Again, much of this shock was absorbed as it was transmitted up the spine to the skull, so that the acceleration of the skull was less than the acceleration at the ankle.

As the subject landed, the mandible initially moved slightly upwards relative to the head as the head tilted forward. However, its inertia then caused it to move about 0.3 mm downwards relative to the maxilla, increasing the separation between the teeth and stretching the jaw-closing muscles. This stimulus evoked a brisk reflex excitation of the masseter muscle at a latency of 7.5 ms after the first detectable relative acceleration of the mandible with respect to the maxilla. The masseter activity was followed by a jaw-closing movement which began about 12 ms after the onset of the EMG response, peaking at 50 ms.

When the same subject now repeated the heel-landing hops with his teeth firmly clenched together (Fig. 1, right column), the maxilla acceleration was similar to the situation when the jaw muscles were relaxed, but the movement of the mandible relative to the maxilla was negligible after landing. The reflex burst of activity in the masseter was abolished, indicating that it was evoked by movement of the mandible and not the head. The reflex is therefore not due to activation of vestibular afferents.

There was no evidence for 'anticipatory' muscle activity before landing in any subject, and the pattern of responses seen was very similar in all subjects.

The mean latency of the reflex measured from the first detectable relative difference in mandibular acceleration with respect to the maxilla during heel-landing was 7.7 ± 0.8 ms (mean ± S.E.M.; $n = 8$), WHICH WAS SLIGHTLY BUT SIGNIFICANTLY LONGER THAN THE 7.4 ± 0.5 MS LATENCY OF THE 'JAW-JERK' REFLEX EVOKED IN THESE SUBJECTS BY TAPPING ON THE CHIN (PAIRED t TEST; $P < 0.02$).

Locomotion

In subjects standing quietly, the mandible remained in a stable vertical position with respect to the maxilla, with the incisor teeth separated by 2–6 mm, and no tonic activity was detected by visual inspection of the raw EMG in the masseter muscle in any subject.

While walking, all subjects touched down first on their heel, after which the sole of the foot came down to contact the treadmill before the take-off into the swing phase of the next step. The raw data recorded in one representative subject while walking at two speeds and running at two speeds on a horizontal treadmill is shown in Fig. 2. The uppermost trace shows the record from the accelerometer

taped to the lateral malleolus of one ankle. Below this are the records of the mandibular acceleration (derived from the difference in acceleration between the maxilla and the mandible), mandibular position relative to the maxilla, and the unrectified EMG signal from one masseter muscle.

The amplitude of the vertical acceleration of the tibia was relatively low in all phases of walking at both speeds (note that the ankle accelerometer shows foot-strikes for only one leg). The high-gain record of the acceleration of the mandible relative to the maxilla shows that during the swing phase of each walking step, there was a small, slow acceleration of the mandible relative to the maxilla: that is, the jaws opened and closed by a small amount as the head moved up and down. This movement was slightly greater at the higher walking speed. However, there were no obvious bursts of masseter EMG with each step, indicating that its stretch reflex was not activated during walking.

During running at both speeds, both the ankle acceleration and the mandibular acceleration following each heel-strike were much larger, as was the vertical displacement of the mandible. The mandible accelerated rapidly downwards about 10 ms after heel-strike (only the alternate heel strikes were registered) and then upwards, and these jaw movements were synchronized with bursts of masseter EMG activity.

The events that occurred following foot-strike are more clearly seen in the averaged records in Fig. 3, which show the various kinematic parameters of the mandibular movement relative to the maxilla, together with the rectified masseter EMG in another subject during walking and running on surfaces with different slopes. Note first that there was little if any tonic activity in the masseter that would support the mandible against gravity under any of the conditions tested.

Slow walking (0.7 m s^{-1}) resulted in a clear downward movement of the mandible following landing in each step. This was greater in downhill walking when the impact of landing was greater, and less in uphill walking when the
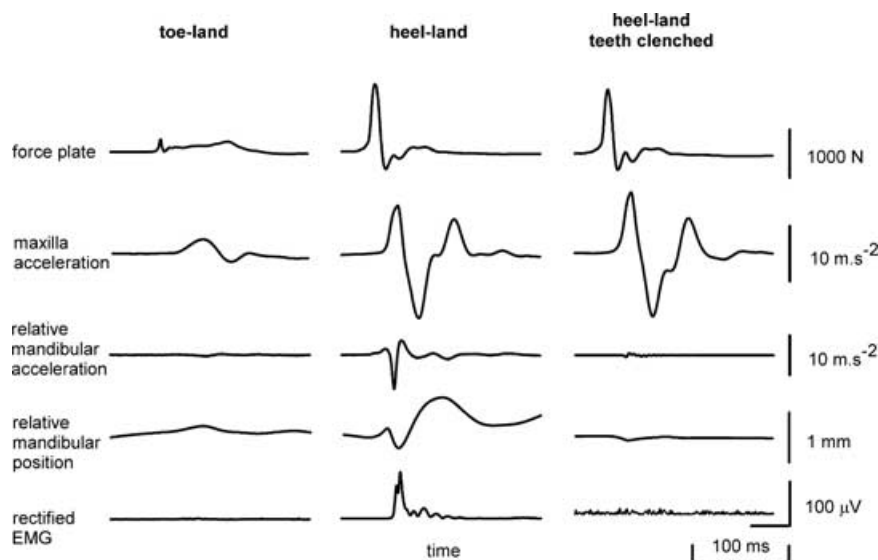

Figure 1. Averaged kinematic and masseter reflex responses during hopping
All records are ensemble averages of data recorded during 100 hops. Data were recorded in a subject hopping on one bare foot and landing on the toes (left), heel (middle), or heel with the teeth clenched (right). The initial deflection in the force plate record shows the instant of landing. Toe-landing induced only slow deceleration of the head (maxilla) and minimal change in the vertical position of the mandible relative to the maxilla (all downward movements shown as downwards), and elicited no reflex response in the masseter EMG. Heel-landing with the masseter relaxed (middle) caused a brisk head deceleration and a downward acceleration of the mandible relative to the maxilla. After moving briefly downwards, the mandible moved briskly upwards, overshooting the rest position: there was no contact between the upper and lower teeth. The downward movement stretched the jaw-closing muscles and evoked the reflex shown in the rectified EMG record. During heel-landing with the teeth clenched (right), there was a large maxilla acceleration as before, but no movement of the mandible relative to the maxilla: the absence of a short-latency reflex in this situation indicates that the reflex response was not the result of a vestibular stimulus (or a movement artefact). Note that, because the mandibular movement was so small during toe-landing and heel-landing with teeth clenched, the averager was triggered with the foot-strike signal from the force plate in those runs.
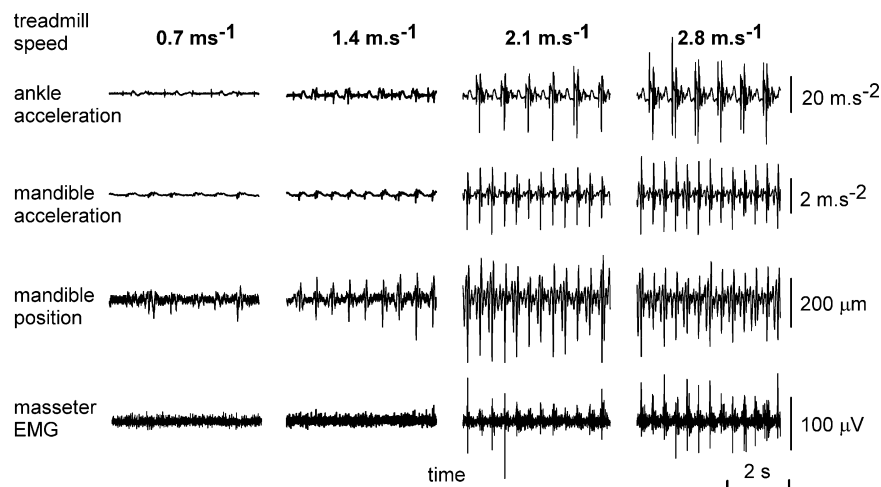
Figure 2. Raw kinematic and masseter EMG data during locomotion on a horizontal treadmill at two walking speeds (0.7 m s^{-1} and 1.4 m s^{-1}) and two running speeds (2.1 m s^{-1} and 2.8 m s^{-1}) Foot acceleration was recorded with an accelerometer on the lateral malleolus of one ankle, so recorded only alternate landings. The record of mandibular acceleration relative to the maxilla was obtained by electronically summing the outputs of the transducers on the upper and lower teeth.

subject landed on the toes: however, these movements did not induce any changes in masseter EMG activity during walking in this subject.

The pattern of responses during running was more complex, and depended on the speed of running and whether the treadmill was inclined upwards or downwards. As in walking, all subjects landed first on their heels when running on a horizontal or downwards-inclined surface, but on their toes when running on the upwardly inclined surface.

When this subject ran at a moderate pace on a level treadmill, the downward acceleration of the mandible after landing was markedly higher, and the mandible moved about 0.4 mm downwards from its original position. The downward movement then slowed and was followed by a

brisk upward movement in which the mandible slightly overshot its original vertical position. This pattern of movement was greater when the subject ran at the same speed on a downwards-sloping treadmill and less when it was inclined upwards. The brisker downward movements during running evoked a burst of activity in the masseter muscles at a latency of about 8 ms (the precise time at which the acceleration began could be estimated only to the nearest millisecond, and the averaging procedure tended to smear the onset time). The amplitude of the EMG response varied with the amplitudes of the mandibular acceleration and position. There was no evidence for inhibitory or longer-latency excitatory reflex responses.

The excitation of the masseter was followed by an upward movement of the mandible to overshoot its
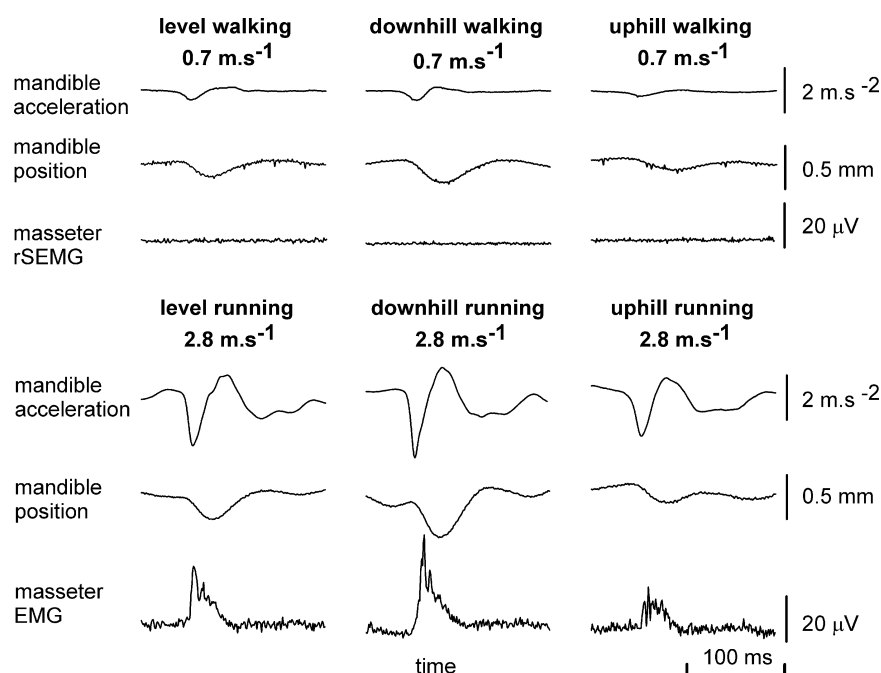

Figure 3. Averaged kinematic and rectified masseter EMG data during locomotion on a treadmill at one walking speed (0.7 m s^{-1}) and one running speed (2.8 m s^{-1}) with the treadmill horizontal, and inclined 5 deg 'uphill' and 5 deg 'downhill' During both walking and running, the downward mandibular movement was least on the uphill and greatest during the downhill trials. However, even downhill walking (in which the subject landed on his heels) did not elicit a reflex response in the masseter in this subject. The amplitudes of the reflex responses during running varied with the amplitude of the downward jaw movement induced on the different slopes.

prelanding position. The mean delay ± s.d. between the onset of the EMG response and the onset of the upward movement of the mandible was 32 ± 7 ms, and the mean onset latency of the reflex measured from the initial downward acceleration of the mandible relative to the skull was 7.3 ± 0.4 ms for all subjects.

Running at different speeds and on different inclinations of the treadmill led to different patterns of acceleration, velocity and displacement (equivalent to stretch of the jaw-closing muscles) of the head and the mandible. These were clearly the result of the different patterns of gait and forces of landing under these different conditions. For example, subjects running downhill landed on their heels, and therefore landed more forcefully (they also fell a little further). This resulted in increased acceleration of the head and hence relative acceleration of the mandible, compared with running on a level surface. On the other hand, when subjects ran 'uphill', they were compelled to land on their toes, and also landed less forcefully (having fallen a smaller distance): this reduced the forces acting on the head and jaw.

The masseter EMG and jaw displacement data from all 12 subjects are summarized in Fig. 4. Walking at the two lowest treadmill speeds produced small amounts of jaw opening and no significant reflex response in the masseter. Running at the two highest treadmill speeds resulted in larger displacements of the mandible, and these were greater for level and downhill slopes than for the uphill slope (Scheffe's test, $P < 0.01$). The peak jaw displacement was similar for the two fastest treadmill speeds. Reflex activation of the masseter was seen after landing when running at 2.1 m s^{-1} and 2.8 m s^{-1}, and this was larger at the higher speed (Scheffe's test, $P < 0.0001$). The reflex was smaller when running uphill compared with running downhill (Scheffe's test, $P < 0.05$), or on a level surface (Scheffe's test, $P = 0.05$).

The different parameters of mandibular movement (peak acceleration, peak velocity and maximal downward displacement) under these different conditions led to scaled reflex responses. Figure 5 shows the data for three subjects recorded for the four treadmill speeds and three inclinations. The lowermost panels show that the peak-to-peak EMG response recorded at stretch reflex latency in the masseter increased monotonically as the treadmill speed increased beyond 1.4 m s^{-1}. However, the kinematic parameters of the downward mandibular movement (upper three panels) did not increase in the same way. At the higher treadmill speeds they reached a plateau value, or even diminished in magnitude.
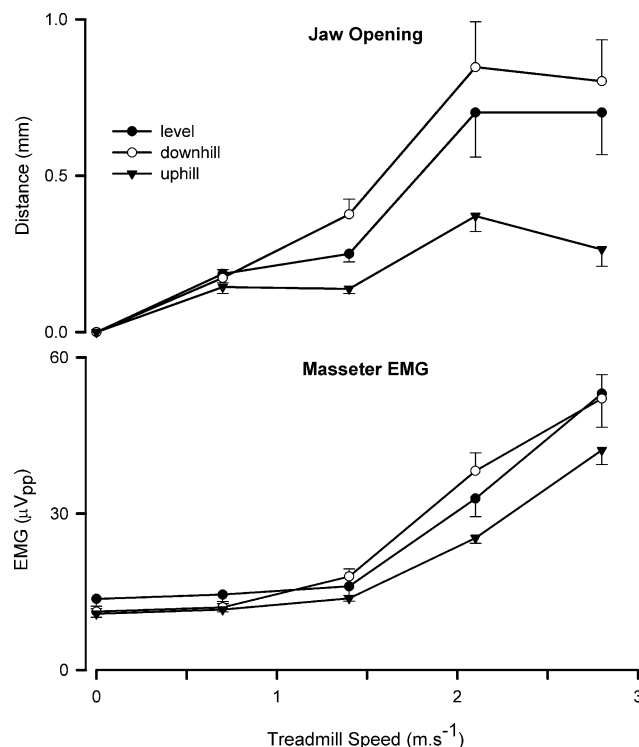
Discussion

The human jaw-closing muscles, particularly the masseter, are richly endowed with muscle spindles (Taylor, 1976; Luschei & Goldberg, 1981), and show clear reflex responses to even very small stretches (Lamarre & Lund, 1975; Poliakov & Miles, 1994). Rapid stretches induce only short-latency (segmental) responses, while slower stretches evoke weaker short-latency responses followed by prolonged longer-latency reflex responses. The latter are similar in appearance to the transcortical reflexes seen in the upper limb (Poliakov & Miles, 1994), but do not involve the motor cortex (Pearce et al. 2003). It is likely that these stretch reflexes give servo-control of muscle length during activities like chewing food, where the resistance to jaw closing changes constantly and cannot be accurately predicted. The stretch reflex acting obversely as an unloading reflex certainly plays an important role in

Figure 4. Effect of treadmill speed and slope on masseter EMG and peak jaw opening after landing

Data are mean ± s.e.m of 12 subjects. Maximal peak-to-peak (pp) masseter EMG and maximal downward displacement of the mandible after landing were quantified from the averaged records of each subject. Both jaw opening and masseter EMG were larger during running (2.1 and 2.8 m s^{-1}) than walking (0.7 and 1.4 m s^{-1}). Jaw opening and masseteric reflexes were smaller with uphill locomotion than in the level and downhill trials. The masseter reflex responses were larger when running at 2.8 m s^{-1} compared with 2.1 m s^{-1}, but peak jaw opening did not differ for these running speeds.

protecting the masticatory apparatus from harm when one bites powerfully on a brittle object that suddenly yields (Miles & Wilkinson, 1982; Miles & Poliakov, 1997). There is also evidence that the stretch reflex system contributes to short-term learning of the appropriate amount of muscle activation necessary to chew a food bolus of varying consistency (Ottenhoff *et al.* 1992*a,b*).

While the function of stretch reflexes in control of the jaw-closing muscles during chewing is well accepted, it has generally been considered that the jaw-closing muscles would not be subject to stretches in the course of normal everyday activities. However, the mandible moves up and down relative to the maxilla during hopping, walking and running (Flavel, Nordstrom & Miles, 2003), indicating that the jaw-closing muscles are subject to stretches during normal daily activities.

Hopping

Normally when hopping on one leg, people land on their toes which is quite comfortable because the antigravity muscles in the ankle, knee and hip absorb much of the shock of the landing. The present study shows that there is minimal vertical movement of the jaw relative to the head after toe-landing and that this does not evoke reflex responses in the jaw-closing muscles. The vertical position of the jaw is presumably maintained by visco-elastic forces in soft landings (Peck *et al.* 2002).

However, in order to hop and land on one heel, the knee must be fully extended and the ankle dorsiflexed. Consequently, much less of the shock of landing is absorbed by the antigravity muscles at the knee and ankle, and the resulting jolt is transmitted to the skull. This is
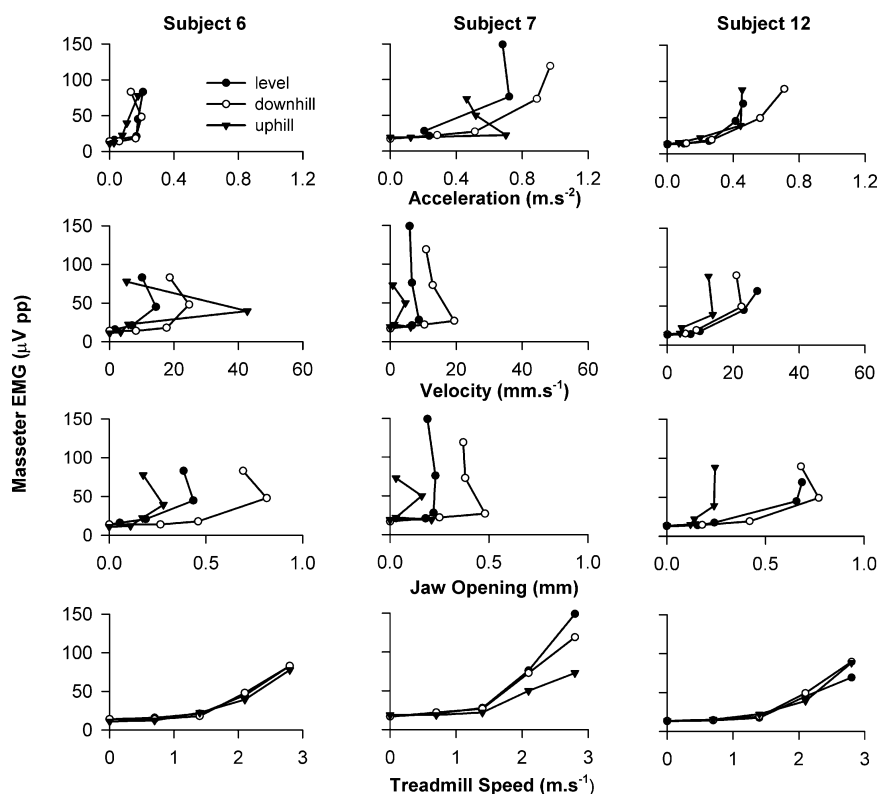

Figure 5. Relationship of the reflex response of the masseter to various parameters of the mandibular movement relative to the maxilla during locomotion at various speeds and inclinations for three subjects
The vertical axis of each graph is the averaged peak-to-peak reflex EMG response in the masseter for a given run. The lowermost panel shows that as the running (i.e. treadmill) speed increased beyond a threshold value, the amplitude of the reflex response increased linearly over the running speeds tested. The upper three rows of panels show the relationships between the various parameters of the mandibular movement relative to the mandible (peak acceleration, peak velocity, maximal jaw opening) and the peak-to-peak (pp) amplitude of the reflex responses recorded at the various running locomotor speeds and inclinations. These relationships are clearly non-linear: in many of the graphs, the value of the kinematic parameter initially increases, then begins to diminish as the reflex response increases. This is evidence that the reflex EMG response in the masseter is influencing the kinematics of the jaw movement, restraining its downward movement during locomotion. Data are given for results during ●: level locomotion, ○: downhill locomotion and ▼: uphill locomotion.

uncomfortable: hence heel-landing is normally avoided during activities such as walking down stairs. Figure 1 shows that heel-landing was followed by a brisk downward movement of the mandible relative to the maxilla: this stretched the masseter, evoking a brisk reflex response in this muscle. The latency of this response is 0.4 ms longer than the monosynaptic reflex elicited by a tap on the chin. The slightly greater latency can be explained by the reduced temporal resolution that occurs when many trials are averaged.

After its downward movement relative to the maxilla, the mandible not only moved upwards but overshot its original vertical position (Fig. 1): however, the teeth did not come into contact in any subject. The overshoot indicates that the upward movement was not solely the result of elastic forces, but must be the result of reflex muscle activation.

The upward movement began about 32 ms after the onset of the masseter EMG. Nordstrom & Miles (1989) have shown that, in low-threshold masseter motor units, i.e. those that are likely to be activated in a stretch reflex (Miles *et al.* 1995), an action potential induces a twitch that peaks at about 38 ms (They could not calculate the electromechanical delay precisely because of the unknown time taken for the motor unit action potential to propagate along the muscle fibres to the intramuscular electrode.) These data strongly suggest that the reflex contraction of the jaw-closing muscles acts in concert with visco-elastic forces to arrest the downward-moving mandible and restore it to its normal postural position.

To exclude the possibility that this reflex is the result of vestibular afferent activation, subjects kept their teeth clenched while heel-landing in one set of trials, thus preventing the jaw from moving and the masseter from being stretched. Figure 1 shows that this abolished the reflex response, indicating that it is not the result of the short-latency vestibulo-masseteric reflex (cf. Deriu *et al.* 2003).

Locomotion

The foregoing indicates that stretch reflexes contribute to the control of jaw posture during an extreme gravitational stimulus, but the more interesting question is whether or not they control the jaw during more conventional activities such as walking and running.

The first suggestion that reflexes contribute to active maintenance of jaw posture was the observation of bursts of jaw-closing muscle activity occurring in each step of cats walking on a treadmill (Lund *et al.* 1984). Shiller *et al.* (2001) recently reported that vertical jaw movements occur during human locomotion, although the mechanisms that maintain jaw posture were not investigated. The amplitude of mandibular displacement during locomotion in humans depends on the speed of locomotion and on the nature of the footfall, i.e. whether landing is heel-first or toe-first (Flavel *et al.* 2003).

In the present study, the jaw-opening that occurred during each step in walking was small and slow, and evoked an irregular reflex response in only three of the subjects tested, and then only at their fastest walking speeds. In pooled data from 12 subjects (Fig. 4) there was no significant reflex activation of the masseter at either walking speed. That is, stretch reflexes do not contribute to mandibular posture during walking. Instead, the small-amplitude, damped oscillations that are induced by the downward displacement of the jaw after landing
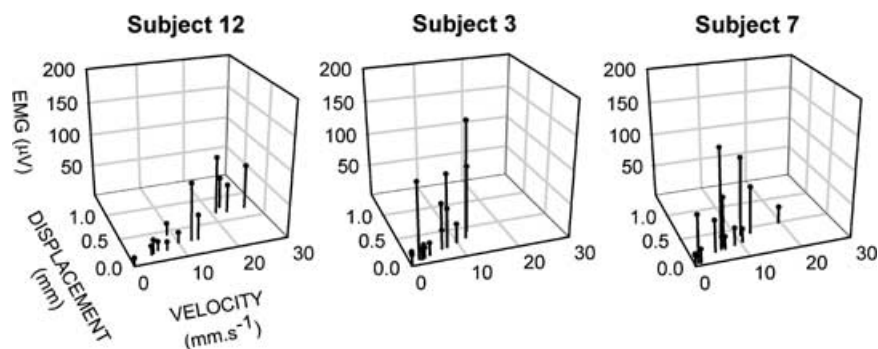

Figure 6. Relationship of the averaged peak velocity and averaged peak displacement of the mandible relative to the maxilla to the reflex EMG response in the masseter in all of the different patterns of locomotion in three subjects
The peak-to-peak amplitude of the averaged masseter response in a given run is plotted against the maximal velocity and maximal displacement of the mandible relative to the maxilla: each data point is shown as a filled circle with a vertical line dropped to the horizontal plane.

suggest that mandibular displacement is minimized by passive visco-elastic mechanisms. This visco-elastic support derives from the soft tissues in the peri-oral area, including the non-active jaw-closing muscles (Peck *et al.* 2002).

However, in a subject who is running, the larger forces transmitted to the skull and mandible by the shock of landing cause the mandible to move more quickly and further downwards relative to the maxilla. This stretches the jaw-closing muscles at higher velocities and higher amplitudes, and evokes clear reflex responses in them (Fig. 3).

The reflex consists of a brief, synchronous discharge in the masseter at a latency of 7.0–9.5 ms (Fig. 3). The latency could not always be measured accurately because of the difficulty in identifying precisely when the downward movement began, particularly in averaged records which reduce temporal resolution. Nevertheless, the latency indicates that the reflex response to the downward jaw movement traverses a segmental, probably monosynaptic, pathway. No evidence for longer-latency stretch reflexes was seen (cf. Poliakov & Miles, 1994; Miles *et al.* 1995).

This reflex excitation in the masseter was followed by an upward movement of the mandible (e.g. Fig. 3). As in hopping, the overshooting of the original jaw position indicates that the upward movement is at least partly the result of active muscle activity rather than passive elastic mechanisms alone, and its timing strongly suggests that the movement was caused by the reflex muscle contraction.

Running at different speeds and on different inclines led to different patterns of forces acting on the mandible and consequently different patterns of stretch reflex responses. In particular, the mandible moved less relative to the maxilla when subjects landed on their toes during uphill running, compared with landing on their heels during downhill and horizontal running (Figs 3 and 4). However, even toe-landing elicited a reflex response during running.

There is no reflex in the masseter during walking at up to 1.4 m s^{-1}, but at faster speeds the reflex increases fairly linearly with running speed (Fig. 4). The relationships between the reflex and the various kinematic parameters of mandibular movement are less clear-cut, as shown in the representative data from three subjects in Fig. 5. In particular, there do not appear to be clear length or velocity thresholds for evoking the stretch reflex in a given subject. That is, it is not possible to draw a vertical line in the jaw-opening (stretch) or velocity panels that indicates a value for mandibular displacement above which the reflex EMG begins.

The amplitude of the reflex response did not always continue to increase in parallel with the amplitude or velocity of the downward movement of the mandible: Figs 4 and 5 show that the maximum amplitude and/or velocity of downward jaw movement often decreased or remained constant when the amplitude of the EMG was larger. The most likely explanation is that these records do not show a stimulus–response relationship of the kind that occurs in the normal laboratory situation where a servo-controlled stretch is imposed on the muscles. Rather, in the freely moving subject, the downward movement of the mandible that stretches the jaw-closing muscles evokes a reflex muscle excitation which then restrains the jaw movement. That is, when the stretch is sufficient to evoke reflex EMG activity, the muscle activation then prevents further downward jaw movement. Stronger stretches evoke more muscle excitation which results in smaller maximal downward jaw movement.

Because there was no clear relationship between either the amplitude or the velocity of stretch and the amplitude of the reflex response, we have plotted the kinematic parameters and EMG data for three representative subjects on three-dimensional axes in Fig. 6. This shows that maximal displacement increased fairly linearly with maximal velocity (shown on the horizontal plane). However, while there was not a clear threshold for the onset of the reflex response, the EMG amplitude increased sharply beyond a certain combination of stretch and velocity, particularly in the subjects whose data are shown in the right and left panels. This pattern is less clear in the central panel, however.

There is a large literature on stretch reflexes in humans as well as in reduced animal preparations (for review see Matthews, 1991). However, most studies have been conducted on the limbs and under highly constrained laboratory conditions in which the stretches have been imposed by a specialized device or by tapping on tendons, with the subject voluntarily regulating prestimulus muscle activity or force. The current experimental situation significantly extends this earlier body of work by examining the operation of a stretch reflex activated under natural conditions. Subjects did not carry out any particular task involving the jaw muscles, and the stretch arose from the downward displacement of the mandible that occurs during normal locomotion. This evoked only the short-latency stretch reflex. The absence of the longer-latency reflex response probably reflects the speed of the stretch. As we showed earlier, slow stretches primarily activate long-latency pathways; however, rapid stretches activate motoneurones at short (segmental) latency, so that they are still hyperpolarized when the long-latency excitatory volley arrives some 35 ms later, and consequently cannot

be brought to firing threshold a second time at the longer latency (Miles *et al.* 1995).

Finally, the observation that the posture of the mandible is not regulated by stretch reflexes in the masseter even during walking in all subjects contributes to the long-standing debate over whether or not such reflexes are responsible for mandibular posture at rest (Woda *et al.* 2001). Together with the evidence from our earlier study (Jaberzadeh *et al.* 2003), this observation strongly supports the conclusion that the mandibular position at rest is not controlled by reflex activation of the masseter: however, we did not record the activity of the other jaw-closing muscles (temporalis and medial pterygoid) so it is possible (although not likely) that activity in these muscles may play a role.

It is concluded that, in a subject who is stationary or walking at a moderate pace, the mandible is supported primarily by passive mechanisms arising from visco-elasticity of the soft tissues in the peri-oral area. However, in a subject who is running, the increased inertial forces acting on the mandible result in larger, faster displacements that trigger short-latency stretch reflexes in the jaw-closing muscles. The size of these reflexes depends on the size and speed of the initial stretch induced in the jaw-closing muscles: hence, the resulting muscle contraction tends to restore the mandible to its prestretch position. Thus, one of the functions of the stretch reflex in the jaw-closing muscles is to maintain and restore the postural position of the mandible when it is perturbed during rapid head movements. The effectiveness of this response is demonstrated by the observation that the maximal downward movement of the mandible was usually less than 1 mm during running. We believe this to be the only situation in which the function of a stretch reflex has been studied under conditions of entirely natural activation.

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